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THE AMERICAN NATURALIST

VOL. XXIV.

OCTOBER, 1890.

286.

THE MESODERM AND THE CŒLOM OF VERTEBRATES.

BY CHARLES-SEDGWICK MINOT.

THE morphology of the mesoderm is one of the most vexed questions of the day. Scarcely an embryologist can be found who has not published opinions on this question considerably at variance with those of most others. It has been maintained that the mesoderm arises from the ectoderm; that it arises from the the entoderm, or from both; from neither, but from two special segmentation spheres; that it has a double origin, part coming from the blastoderm, part from the yolk; and even that there is no mesoderm.

We now know positively that in all vertebrates there is a distinct and unmistakable mesoderm, which spreads out from the primitive streak in all directions, and has distinctive histological characteristics. Two large cavities appear in this mesoderm on either side of the median axial line. The mesodermic cells which bound these two cavities assume an epithelial arrangement, and are designated as the *mesothelium*; the cavities constitute the *cœlom*; the remainder of the mesoderm is known as the *mesenchyma*, and corresponds to the embryonic connective tissue of older writers. The mesothelium at various points throws off cells, which are added to the mesenchyma. We have accordingly two distinct phases to study, viz., the origin of the mesoderm, and the differentiation of the mesenchyma and mesothelium, and together with the latter the formation of the cœlomatic cavities.

I. ORIGIN OF THE MESODERM.

Mesoderm of Elasmobranchs.—In the cartilaginous fishes the mesoderm arises from the entoderm close to the ectental line. The observations of Balfour in his monograph, 2 (see also his works, I., 246–268), established the fact that the mesoderm appears after the two primary layers and is connected with the entoderm. This fact has since been abundantly confirmed (see Kollmann, 25; Swaen, 41; Rückert, 32, 33; Rabl, 29; D. Schwarz, 36, et al). These later observations, particularly those of Rückert and Rabl, have settled the exact point, or rather area, of entoderm which is mesoblastogenic. Unfortunately Rabl overlooked the phenomena of concrescence, and consequently reached conclusions as to the development of the mesoderm which I feel no hesitation in pronouncing erroneous. The mesoderm is differentiated along the embryonic rim before concrescence takes place; hence, when concrescence is partly completed, there is an axial stretch of mesoderm, and from the hind end of this the mesoderm spreads out toward each side along the embryonic rim in connection with the entoderm, as has been described.¹ We can distinguish the axial mesoderm from the lateral mesoderm; but later on, when concrescence has progressed further, there is no lateral mesoderm, for it has become axial. Rabl, however, failed to study the later stages, and so came to consider that this temporary condition of the mesoderm signified a double origin; accordingly he distinguishes between the “gastral” (axial) and “peristomal” (lateral) mesoderm, and makes the unsuccessful attempt to show that the “gastral” and “peristomal” mesoderms are of essentially different origin in all vertebrates. Had Rabl accepted the law of concrescence, he would certainly have not fallen into these errors. There is no evidence whatever that there is an evagination of the entoderm, as the Hertwigs maintain can be shown in the amphibians (see below). On the contrary, the cells grow forth from the entoderm, so as to constitute a sheet between the primary germ-layers. Soon the connection with the entoderm is permanently severed.

¹ AMERICAN NATURALIST, 1890, p. 507.

The fact that the mesoderm appears first in the embryonic rim renders it easy to make sure of its springing from the entoderm. Later, when concrescence moves the rim into the axial line, all three germ-layers are united in the axis of the primitive streak, and it becomes more difficult to decide which of the layers the mesoderm is specially connected with. To conclude: In Elasmobranchs the mesoderm arises over a limited area of the entoderm near the ectental line; it separates from the entoderm apparently by a process of delamination, but the exact means of separation have yet to be investigated; it remains for a while connected with the entoderm along the embryonic axis; after its separation from the entoderm the mesoderm expands by proliferation of its own cells, and receives no accretions from the yolk, so far as at present known.

Mesoderm of Teleosts.—So far as the published accounts go the middle layer of bony fishes arises, as maintained by Balfour (*Comp. Embryol.*, II., 74), from the entoderm. Such appears to be the significance of Ryder's observation, 34, 41, of A. Goette's, 9, E. Ziegler's, 45, Agassiz and Whitman's, 1, and of others. For a good description, together with citations of conflicting authorities, see M. Kowalewski, 26, 469–474. Apparently the blastodermic rim is turned under, and the turned-under portion yields the entoderm, and is intimately connected with the sheet of mesodermal cells, very much as in sharks; the mesoderm is several layers thick, and extends under the ectodermal blastoderm, gradually thinning out; the cells of the middle layer are at first closely compacted.

Mesoderm of Amphibia.—Here it seems also clearly established that the mesoderm arises from the entoderm, principally along and alongside the median line, as a sheet of cells with no cavity (cœlom) included between them; along the axis of the primitive streak and at the blastoporic margin the connection between the mesoderm and the entoderm is both evident and intimate (see Bellonci, 5, Tav. II., for figures showing this point in the axolotl, and O. Schultze, 35, for similar figures of *Rana fusca*). These facts have been recorded by so many observers that there can be little doubt or none of their entire accuracy (see the description

and cuts, *ante* p. 618). It may be considered as still uncertain whether the sheet of mesoderm receives accretions at its distal edge from the yolk cells (entodermic) upon which it rests. There usually is no sharp limit between the two, and therefore we must consider it probable that at first the mesoderm receives additions from the yolk; later on it is found divided from the vitelline cells, and after it has split off it probably grows independently. The growth of the mesoderm at first from the yolk has been found in *Petromyzon* by A. E. Shipley, 38, 177-178 (of Studies), although in later stages the mesoderm is severed from the yolk.

In later stages the mesoderm is wanting in the median line, and thus constitutes two masses or two lateral sheets. This bilateral division is effected by the development of the medullary groove and notochord. The mesodermic connection with the entoderm is retained, but is double, owing to the division. Along the median dorsal line of the archenteron runs the strip of entoderm which forms the notochord; on each side of this strip runs the line of connection between entoderm and mesoderm. The study of this *secondary* condition has led many authors into the

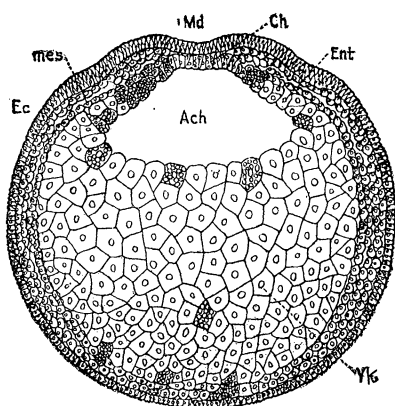


FIG. 23.—Axolote embryo: transverse section of an early stage; after Bellonci. *Ec*, ectoderm; *mes*, mesoderm; *Md*, medullary groove; *Ch*, notochord; *Ent*, entoderm; *Ach*, archenteron; *Yk*, yolk.

error of ascribing a double origin to the amphibian mesoderm, and inferentially to the vertebrate mesoderm in general. This brings us to the consideration of O. Hertwig's views, which form one of the chief supports of the "Cœlomtheorie" of the brothers Hertwig. For further discussion of this theory, see p. 893.

O. Hertwig, 12, 13, studied stages in which the notochord had appeared, and at this time, as O. Schultze, 35, has shown, the primitive relations of the layers no longer exist, but Hertwig regarded the secondary arrangements in question as primary. He found no meso-

derm in the axial line above the notochord; at the edge of the notochord, where it joins the undifferentiated epithelial entoderm of the archenteron, there is on each side a groove which in cross sections appears as a notch (Fig. 23); the notch is of variable depth, is sometimes absent, and is a temporary feature. In the neighborhood of the furrow, alongside the notochord, the mesoderm is still intimately connected with the entoderm. These relations are believed by Hertwig to indicate that the mesoderm arises as two masses, which is not the case, and that each mass is really a diverticulum of the archenteron, the furrow being the mouth of the diverticular cavity. Hertwig's figures, 12, Taf. XIII.-XIV., offer the plainest representations of the mesoderm in Triton as paired diverticula; but these figures² are evidently digramatic, and they must be termed inaccurate, I think, in the very respect which are essential to Hertwig's theory. This appears from the investigations of Götte, 10, Bellonci, 5, Bambeke, 3, O. Schultze, 35, and others; compare also K. Lampert, 27. The reader may compare, for instance, Hertwig's Fig. 10, *l.c.* Taf. XIII., with Bellonci's Fig. 11, *l.c.* Tav. III. O. Schultze's detailed criticism, *l.c.* 344-349, of Hertwig's account seems to me entirely justified, and I accordingly accept it as a complete disproof. This criticism shows that Hertwig's conception is based upon insufficient and erroneous observations; insufficient because he did not investigate the early condition of the mesoderm, and failed to recognize the fugitive and unessential character of parachordal grooves; erroneous because the cavity in the mesoderm does not really communicate with that of the archenteron. There are other errors, which Schultze points out, and which are important.

We find in amphibia, at a certain stage, the axial (Rabl's gastrales) and lateral (Rabl's peristomales) mesoderm. The former is in the region of the completed concrescence, the latter around the edge of the anus of Rusconi. The former is connected with the entoderm alone; the latter with the ectoderm also, since the entoderm is connected with the ectoderm around the uncon-

² Some of them are reproduced in Hertwig's *Lehrbuch der Entwicklungsgeschichte*, sechstes Capitel.

crested blastoporic rim. The connection with the ectoderm renders it possible that the middle layer receives cells from the outer layer, but there is no direct proof of this. When the concrescence is completed the mesoderm severs in the posterior axial region its connection with the entoderm, but retains awhile its connection with the outer germ-layer. The same phenomenon recurs in the amniota. It cannot, however, be taken to signify that the middle layer originates from the ectoderm, since at an earlier stage it is clearly entodermal.

Mesoderm of Sauropsida.—We may consider reptiles and birds together, since the early history of the mesoderm is very similar in the three classes. In *birds*, the exclusively entodermic origin of the mesoderm is in my opinion conclusively demonstrated by the researches of Duval, 8, 104–117; the entoderm gradually thickens by migrations of its cells over a considerable axial area; the upper stratum of this thickened area separates off as the mesoderm, except that in the axial line it retains its connection with the entoderm; when concrescence takes place, the three layers are of course united in the axial line, and hence, as shown by Duval, the mesoderm is connected with the ectoderm. Hence we have two axial regions: 1°, the region of concrescence, characterized by the union of the mesoderm with the ectoderm, and known as the primitive streak; a little later the connection between the mesoderm and entoderm is lost in the posterior part of the streak, but retained in the anterior part; 2°, in front of the streak the region of completed concrescence known as the head-process, in which the mesoderm is united with the entoderm only. The secondary stage is the one best known through the investigations of many embryologists. It forms the starting of Rabl's investigations, 29, 129–140, who accordingly failed to recognize the true origin of the mesoderm, having mistaken a secondary for a primary condition. After the mesoderm is once separated from the entoderm, it apparently receives no further cells from it, except in the axial region; it is not improbable that along the primitive streak cells are also thrown off from the ectoderm and added to the mesoderm.

In *reptiles*, so far as our present unsatisfactory knowledge enables us to judge, the development is similar; that is to say,

the mesoderm arises by delamination from the entoderm, but remains connected with it along the axial line in front, *i.e.*, in the head-process it remains connected with the entoderm only, but along the primitive streak it becomes secondarily connected with the ectoderm. After its delamination the mesoderm expands independently of other germ-layers, except along the axis. That the relations are like those in birds has been shown clearly by Strahl, 39, and also by Weldon, 43, whose figure is reproduced (*ante* p. 714, Fig. 22, A). The intimate connection of the mesoderm with the entoderm at the blastodermic rim before concrescence is sufficiently established by Kollman, 23, 403-406, though his conception that this part of the mesoderm is a separate structure, which he terms *akroblast*, renders it difficult to follow certain parts of his description. C. K. Hofmann may also be cited, though his account (Bronn's *Thierreich*, Reptilien, p. 1881) is of doubtful accuracy in several respects. L. Will, 44, 1127, finds that in the Gecko the mesoderm is united with the entoderm in the head-process, but omits to describe its exact connection with the primitive streak; the stages showing the *origin* of the mesoderm he does not mention. The processes involved will undoubtedly be understood as soon as the concrescence of the axis has been worked out,—a fundamental question which as yet not a single investigator has heeded.

Mesoderm of Mammals.—In this class, according to the best recent investigations, the mesoderm appears to have a distinctly two-fold origin. According to Bonnet, 6, 196, part of the mesoderm grows out from Hensen's knot, at a time when the knot is a thickening of the ectoderm, and has not yet acquired any connection with the inner layer; another portion is produced peripherally (Fig. 18 *ante* p. 705) by delamination from the inner layer; the two anlagen grow toward one another, and unite into one continuous mesoderm, in which all trace of the primitive double origin is obliterated. Kölliker has recorded (Würzburger Festschrift) the outgrowth of the mesoderm from Hensen's knot in the rabbit, and his statement has been confirmed by Fr. Cariuș, 7, 17. In later stages we find the relations of the layers similar to those in Sauropsida, there being a head-process with the mesoderm

connected axially with the inner layer, and a primitive streak in the front part of which the three layers are connected axially, and in the hinder part of which the middle layer is connected with the outer layer only. This stage is quite well known; cf., Heape, *II*, on the mole; Bonnet on the sheep, *6*; Kölliker on the rabbit (*Grundriss*); Selenka on the opossum, *37*; Lieberkühn, *28*, and others; especially the very careful descriptions of the rabbit's layers by C. Rabl, *29*.

Now, we do not yet understand the homologies of the mammalian blastodermic vesicle, hence we cannot explain the peculiar relations of the mesoderm to Hensen's knot, as the homology of the knot is unknown. However, since mammals are in all respects related to the Sauropsida, and especially since there is a close likeness between the subsequent stages of the two classes, it is probable that the origin of the mammalian mesoderm will be shown ultimately to be essentially the same as in reptiles. At present it seems to me impossible to offer any satisfactory interpretation of the observed double origin of the mammalian mesoderm.

The Vertebrate Type of Origin of the Mesoderm.—The preceding paragraphs show that in all classes of vertebrates the origin of the mesoderm is essentially the same, *except* in the mammals. The relations in the mammals we do not understand. In the non-mammalian vertebrates the mesoderm first appears as a thickening of the entoderm over a not inconsiderable area around the concrescing blastodermic rim, and it becomes separated from the entoderm by the gradual parting of the upper cells to form the true mesoderm from the lower cells or permanent entoderm; this delamination does not take place next the blastodermic rim (or after concrescence in the axial line), hence in the region of the primitive streak the three layers may be connected for a time; further in the prolongation of the axis in front of the streak the mesoderm does not separate from the entoderm, thus forming the head-process. It is important to note that the mesoderm arises over a considerable area during the same period; that its formation may be more or less advanced before concrescence of the rim; and that after concrescence it stretches across the axis of

the embryo between the ectoderm and entoderm, thus becoming a continuous sheet or layer. This fact, that the mesoderm is a single anlage, needs to be specially emphasized. So far as known to me, there is not a single vertebrate which has been shown to lack this stage; but on the contrary, its occurrence is established for all classes, and by so many observers, that we may well assert that there are few facts in embryology better established. Later on the mesoderm becomes divided in the axial line, and a too exclusive consideration of this secondary condition has led to several theories of the mesoderm, which would hardly have been brought forward had their authors not neglected to take into account the earlier condition of the middle layer. Some of these theories are discussed below.

After its delamination the mesoderm is a distinct layer, and grows independently, receiving no accretions from the other layers, except in the axial line, where it receives cells from the entoderm, and in the region of the primitive streak. The edge of the expanding sheet of mesoderm is free, as has been pointed out in the previous chapter, resting upon the yolk, but not fused with it. It is, therefore, it seems to me, impossible to admit that there is a peripheral ingrowth of tissues arising from the yolk, and entering the mesoderm to form the blood, etc. (compare below, *Theories of the Mesoderm*).

The origin of the mesoderm in *Amphioxus* and invertebrates differs in many respects from that in vertebrates, and no attempt to establish the homologies of the processes throughout the animal kingdom has been successful. I accordingly merely give a brief notice of the mesoderm of *Amphioxus*, adding a mention of the mesodermal bands of invertebrates.

The ovum of *Amphioxus* is discharged from the body and impregnated externally; it is about 0.105 mm. in diameter, and as it contains only a small amount of yolk undergoes a holoblastic segmentation, which results in a well-marked blastula stage (Fig. 24), followed by a gastrula stage. The gastrula elongates, the blastopore remaining open at the posterior extremity. Differentiations now take place, by which the ectoderm forms the axial anlage of the nervous system, and the entoderm pro-

duces the notochord and the mesoderm; the three processes going on simultaneously. The accompanying Fig. 24 represents a cross section of a larva with segments. The ectoderm, *Ec*,

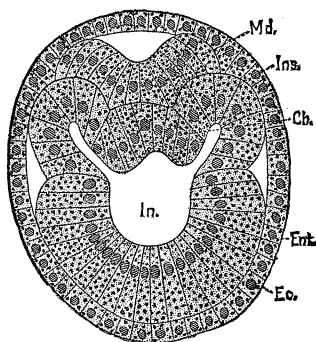


FIG. 24.—Transverse section of an *Amphioxus* embryo; after Hatschek. *Md*, medullary plate; *Ch*, notochord; *Ent*, entoderm; *Ec*, ectoderm; *In*, archenteric cavity; *Ms*, mesodermic segments.

everywhere bounds the section; on the dorsal side a portion of the ectoderm has been separated off to form the medullary plate, *Md*, above which is a small cavity. The cavity, *In*, of the archenteron is irregular, but symmetrical in outline; the entoderm bounding it can be separated into four parts: 1°, the lower portion, which forms the permanent entoderm, *Ent*; 2°, the upper median portion, which becomes the notochord, *Ch*; 3°, 4°, two lateral portions, constituting the diverticula, *Ms*; each diverticulum is a separate pouch, and as the development progresses, there are

formed a series of pairs of pouches, stretching on either side along the notochord; later the pouches separate altogether from the archenteron, each becoming a closed sack; the first pair of pouches, however, retain their connection for a considerable period with the archenteron, and have been described by older writers as glandular organs. The development of the pouches is, with the exception noted, most advanced anteriorly, and as we go tailwards the pouches are less and less advanced in development, until, as shown in Fig. 25, they merge into the general entoderm as a band of cells, *Mes*; the last of which is the "mesoblast," *Mb*, a large granular cell, quite distinct from the remaining cells of the band or pouches. The pouches are the primitive segments (Ursegmente, mesoblastic somites of Balfour). In *Amphioxus*, then, the mesoderm arises from the entoderm along two lines, and is divided into paired hollow segments before it is separated from the mesoderm. Some writers, especially the brothers Hertwig, think this process of development to be primitive, and that the vertebrate type is derived from it. In true ver-

tebrates the mesoderm arises on each side, but also in the axis, and becomes two masses, when the medullary groove and notochord appear. In *Amphioxus* the medullary plate and notochord appear very early, and the division of the mesoderm may be due to that fact. *Amphioxus* is undoubtedly a lower type, but whether it really preserves the older type of development in its purity is doubtful; indeed, it is probably a tunicate rather than a vertebrate.

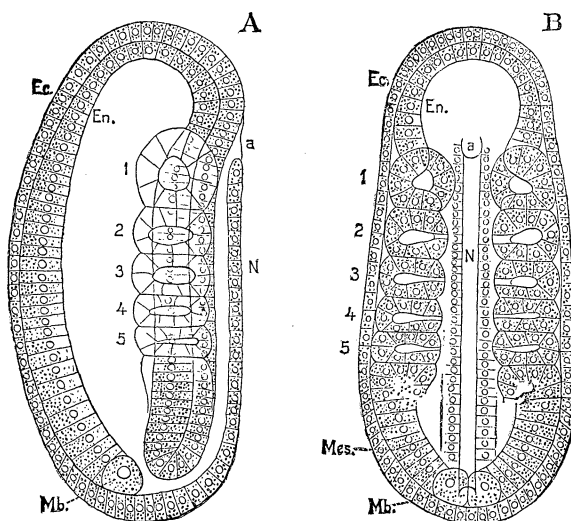


FIG. 25.—*Amphioxus* embryo; after Hatschek. A, side view; B, ventral view. *Ec*, ectoderm; *En*, entoderm; *a*, neuropore; *N*, nervous system; *Mes*, mesoderm; *Mb*, mesoblast; 1-5, segments.

Hatschek, in a series of brilliant investigations, has shown that in many bilaterally symmetrical invertebrates the mesoderm arises as two bands of cells, which subsequently divide into a series of closed sacks (segments), and which, during their own formation, terminate each in a single large posterior cell (mesoblast), which throws off cells to add to the mesodermal band (germ-band, Keimstreif). This "mesoblast" by its appearance and position appears to be a derivative of the entoderm. As a matter of speculation, we may assume that in *Amphioxus* we have the germ-bands, but characterized by an exceedingly precocious segmentation. We can further assume that in vertebrates

we have the germ-bands also, but that they are modified, 1°, by the loss of the distinct terminal mesoblast; 2°, by precocious fusion in the axial line; and 3°, by extremely retarded segmentation. A great deal may undoubtedly be said in favor of these two assumptions, which together constitute the only "THEORY OF THE VERTEBRATE MESODERM" which of the many theories which have been advanced is at all likely, in my opinion, to prove of permanent value.

Expansion of the Mesoderm.—After the mesoderm is once formed as a distinct layer, without connection with the primitive layers except in the axial line, it expands independently,—that is, by the proliferation of its own cells. During its early expansion

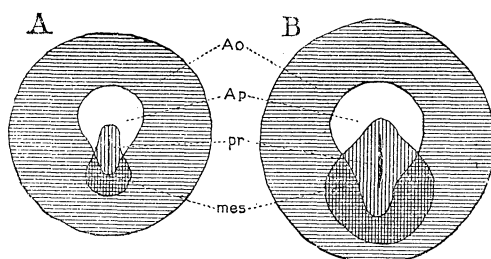


FIG. 26.—Diagrams of the embryonic area of the chick. *Ao*, area opaca; *Ap*, area pellucida; *pr*, primitive streak; *mes*, mesoderm. After Duval.

the mesoderm assumes in all amniota a definite series of characteristic outlines. It is at first pear-shaped (Fig. 26, A), the anterior end being pointed; it extends a short distance only in front of the primitive streak, and is widest a little distance behind the area pellucida, *Ap*. The same stage is found in mammals (see Kölliker, *Grundriss*, p. 93, and Fig. 71). The condition in the chick at about the twentieth hour of incubation is indicated by Fig. 26, B, drawn on the same scale as A, and at the close of the first day by Fig. 27. In the last-mentioned figure it will be noticed that the mesoderm is expanding unequally in front, having sent out two lateral wings, which leave a median space between them without mesoderm. These wings continue their growth, and finally meet in front, so that in the anterior part of the area pellucida there is a small tract without any mesoderm, although there is mesoderm all around it. This tract is the pro-

amnion, of which I shall give a fuller history elsewhere. The expansion does not take place by any means with the exact regu-

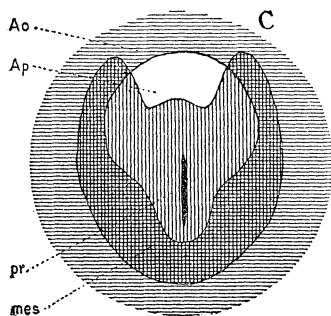


FIG. 27.—Diagram of the embryonic area of a chick. *Ao*, area opaca; *Ap*, area pellucida; *pr*, primitive streak; *mes*, mesoderm.

larity indicated by Figs. 26 and 27, but, on the contrary, in birds, as shown by Zumstein, 46, the outline of the middle layer is always irregular and more or less asymmetrical. Although there are not yet many observations available as to the outline of the growing mesoderm, yet it is probable that the preceding description is essentially correct, not merely for birds but for all amniota. It is certainly so for the rabbit (Van Beneden et Julin, 4).

II. FORMATION OF THE CŒLOM.

Early in the course of development there appear in the mesoderm two large cavities, one on each side, which together constitute the *cœlom* or embryonic body cavity. In the adult mammal the cœlom is represented by the pericardial, pleural, and abdominal cavities; the cœlom also gives rise to the cavities of the muscular segments (protovertebræ), and probably also to certain tubular parts of the urogenital system. But, although its subsequent changes are complex, when it first appears the cœlom consists of a pair of fissures in the mesoderm.

Only one precise account of the development of the cœlomatic fissures is known to me, namely, that of Bonnet, 6, 202, for the sheep at about thirteen days. Around the embryo, at some distance from the axis, there appear a series of irregular fissures of rounded or elongated form, which may in part open on the mesodermic surface; gradually the fissures enlarge and fuse, at the same time becoming more closely bounded by the mesodermic cells; thus there arises a continuous cavity in the mesoderm, which is for a time crossed by cells and cell processes; meanwhile the cells which are loosely put together form a compact layer of epithelium bounding the cavity, which we can now designate as the *cœlom*, or primitive body cavity. By similar

processes the coelom grows toward the axial region, but never penetrates it, the primitive streak and head-process never developing a coelom. The changes which have taken place have now divided the mesoderm into two tissues: 1°, the *mesothelium* or epithelial lining of the body cavity; 2°, the *mesenchyma* comprising all the non-epithelial mesoderm. Whether in all cases the coelom begins as a series of small spaces, which subsequently fuse, we are unable to say; but it is by no means improbable that such is the case. It is, I think, also probable that the coelom begins always to appear at a little distance from the embryo, and spreads both centripetally and centrifugally. In the sheep the large size of the coelomatic cavity is connected with the precocious development of the amnion.

Of other vertebrates we can say only that the coelom appears, and is at first merely a narrow fissure. It divides the mesoderm into an upper leaf (*Hautfaserblatt*) and an inner or lower leaf (*Darmfaserblatt*); the former may be called the *somatic*, the latter the *splanchnic mesoderm*, as proposed by Balfour. The upper leaf lies close against the ectoderm; the two layers together form the *somatopleur*, or body wall. The lower leaf lies close against the entoderm; these two layers together form the *splanchnopleur*, or wall of the alimentary tract. Both the somatic leaf of mesoderm and the splanchnic comprise mesothelium and mesenchym; axially the two layers become continuous, both with one another and with the axial mesoderm. The mesothelium continues for some time to throw off cells, which add themselves to the mesenchym, but except for this the two tissues have each an entirely separate history, and the adult tissues derived from them form two well-defined and natural groups.

The morphology of the coelom is so important that it is difficult to understand why so many investigators have slurred over the question of its embryonic development. Exact observations on its first appearance and on the first stages of its expansion in various types are urgently needed, and would certainly do more than anything else to throw light on the still obscure problem of the origin of the mesoderm.

*Theories of the Mesoderm.*³—From the time of Von Baer's *Entwicklungsgeschichte*, of which the first part appeared in 1828, until 1868, when W. His's great monograph on the chick, 16, was published, embryologists recognized the three layers, and regarded the mesoderm as a natural unit. His led the way to our present conception by a little-known article, 15, on the membranes and cavities of the body, and his monograph, 16, above mentioned fully established the necessity of recognizing two main groups of mesodermic tissues. Accordingly he divided the mesoderm into two parts, the *archiblastic*⁴ and *parablastic*, corresponding respectively essentially to mesothelium and mesenchyma. Under archiblast, His included not only the mesothelial tissues proper, but also the smooth or organic musculature; under parblast the mesenchymic tissue, except the smooth muscle. The terms used corresponded to his theory of the origin of the two parts of the mesoderm, for he believed that the archiblast arose in the axial region, and was contained in the embryo from the start, while the parblast arose peripherally, and grew in towards the embryo, a conception which was perhaps suggested by the appearance of the blood-vessels first outside the embryo proper. Seeking still further for the source of the supposed peripheral parblast, he believed he had found it in the germinal wall. The study of the relations of the wall in the chick induced him to think that the elements of the white yolk became parblast cells; moreover, the study of the hen's ovary led him to the conclusion that the white yolk was developed from the granulosa cells, and that these cells arise from leucocytes. He thus traced back the parablastic cells to maternal leucocytes. It has been shown that the granulosa cells are not leucocytes, and that the granulosa cells do not enter the ovum; the white yolk-grains never become cells, for it has been proved that all nuclei of the segmentating ovum come from previous nuclei, and lie in protoplasm, not in the yolk-grains; and finally it has been shown in this chapter that the mesoderm arises, as a whole, not from double sources. Professor His's views as to the origin of the parblast

³ See *ante* p. 880.

⁴ His's archiblast includes the ectoderm, entoderm, and archiblastic mesoderm.

must, in my judgment, be given up; but this is no reason for overlooking, as certain writers have done, the fundamental significance of the distinction drawn between the two primary groups of mesodermic tissues. Subsequent research has made only one important change necessary, namely, the transfer of smooth musculature from one group to the other. In view of this change and of the fact that parablast has been used with various other meanings, and of the unaptness of His's names, since we renounce the theory they correspond to, it will be well to use exclusively the newer terms mesothelium and mesenchyma.

The parablast theory has been defended by His, 17, and modified by him, 18. At present he holds to the distinction originally drawn, but is inclined to withdraw his hypothesis of the origin of the parablast. A number of writers have agreed with His as to the separate peripheral development of the mesenchyma (parablast). Among those may be mentioned Rauber, 30, 31, and several authors who have dealt with the development of the blood. The most important of the disciples of His is Kollmann, who, in a series of articles, 22, 23, 24, 25, has maintained the double origin of the mesoderm. Of these papers the most important is that on the "Randwulst," or germinal wall, of the structure of which in the chick it gives an excellent description. Kollmann regards the germinal wall not as a part of the entoderm, but as a distinct organ composed of segmentation spheres, and destined to produce blood-vessels with blood, and probably also connective tissue; this peripheral anlage (Randkeim) he designates as *acroblast*, and the single cells derived from it he names *poreuten*. Waldeyer, 42, has accepted the parablast theory, but with a modification by which he seeks to reconcile conflicting observations. His article is written with characteristic clearness and exhaustive mastery of the literature, and will be found especially valuable by those who wish to pursue this subject further. Waldeyer distinguishes between the primary and secondary segmentation; the former producing the ectoderm, entoderm, and archiblastic mesoderm; the latter occurring later, and giving rise to the parablast. This remnant of the ovum in holoblastic ova consists of cells; in meroblastic ova of

egg protoplasm, which has its cell division (segmentation) retarded, and the cells, whether early or tardily produced, immigrate into and between the germ-layers already developed.

The opposition to the parablast theory is the sum of numerous observations which, as pointed out in the previous part of this chapter, prove, it seems to me, that the mesoderm arises in all vertebrates (except mammals?) as a unit, and subsequently separates into mesothelium and mesenchyma. The leading opponent of the separate origin of the parablast is Kölliker, in both his textbooks (*Entwicklungsgeschichte*, etc., and *Grundriss*), and in separate articles (see especially 19, 20, and his criticism, 21, of Kollmann). I agree with Kölliker that it has been sufficiently demonstrated that the "acroblast" belongs to the entoderm, and that after delamination of the mesoderm the acroblast is transformed into the epithelium of the yolk-sac; for a conclusive demonstration that this is so in reptiles, see H. Strahl, 40.

The *cœlom theory* of the brothers Hertwig includes a fundamental modification of the parablast theory. The main features of the cœlom theory are not original with the Hertwigs, but may be found in previous writers. Nevertheless, they were the first to present the theory in a complete formula, and with a backing of facts, both new and collected from others, so extensive as to compel attention. In justice to E. Ray Lankester it must be stated that he is really the author of the cœlom theory, having, in 1877 (27, A), published the hypothesis that the cœlom is derived from the archenteron, and that the mesoderm of vertebrates represents solid entodermal diverticula. It is unfortunate that the Hertwigs have not made due acknowledgment of what they owed to Lankester and others. They made a series of investigations on the germ-layers of various representatives of the animal kingdom, and presented their general results in a comprehensive article (O. and R. Hertwig, 14). O. Hertwig has again expounded the theory in his text-book of embryology. The cœlom theory consists of two parts: 1°, the cœlom is formed by diverticula of the archenteron and its lining; the mesothelium is part of the entoderm; 2°, the mesenchyma consists of cells thrown off by the germ-layers, and is essentially distinct from the

mesothelium. The value of this theory lay in the clearness of its formulation, thus facilitating discussion, and also in its bringing out the difference more clearly between the epithelial and the non-epithelial portions of the mesoderm. As we have seen, there is no evidence of a character to render even probable that part of the cœlom of vertebrates represents archenteric diverticula; the whole mesoderm appears as a single germ-layer, which is subsequently differentiated into mesenchyma and mesothelium. Hence both essential parts of the cœlom theory are inapplicable, at least in the present state of our knowledge, to vertebrates. For further discussion of the difficulties of the Hertwigs' theory, see Rabl, 29, 198-202. The Hertwigs recognized the significance of the parablast, and added the important rectification, which Flemming's observations had already rendered necessary, of separating the smooth muscles from the striated skeletal muscles, a separation the propriety of which was wrongly questioned by Balfour (*Comp. Embryol.*, II., 359). By this advance the two groups of mesodermal tissues became properly delaminated.

C. Rabl's theory of the mesoderm is based, it seems to me, wholly upon his failure to understand the law of concrescence. That the mesoderm appears (perhaps in all vertebrates) while concrescence is going on is well ascertained; consequently there is an axial mesoderm (Rabl's "gastrules mesoderm") where concrescence has taken place, and a lateral mesoderm (Rabl's "peristomales mesoderm") in the part of the blastodermic rim which has not concresced. Until Rabl proves that his "peristomales" mesoderm does not become axial mesoderm in later stages, his theory can have no standing. His memoir brings out one point of very great importance for the elucidation of the early stages of vertebrates, namely, that the "peristomal" mesoderm—in other words, that of the blastodermic rim in selachians and of the lips of the anus of Rusconi in amphibians—is represented in the amniota by the mesoderm of the primitive streak. If this interpretation, which is much strengthened by L. Will's researches on the Gecko, 44, be verified, then the primitive streak is the homologue in amniota of the anus of Rusconi, and is the region where concrescence is incomplete; the head-process is

then the part where concrescence is finished. This concords with the observed fact that the head-process grows at the expense of the primitive streak, as it would do if concrescence continued.

The So-called Parablastic Nuclei of the Yolk.—In meroblastic vertebrate ova, after the embryo is formed, there appear in the yolk near its surface, underneath the extra embryonic blastoderm, peculiar large nuclei, which are commonly designated as the parablastic nuclei. The following description applies to *Pristurus*.⁵ The extra embryonic ectoderm is a rather thin, much-flattened epithelium lying close to the yolk; below the ectoderm is the superficial layer of the yolk, a broad stratum of protoplasm with scattered small yolk-granules; a little deeper down a row of irregular vacuolar spaces, and again, a little deeper, a layer of very big nuclei, each with a distinct intra-nuclear network and several deeply stained nucleoli; the nuclei vary in size, being from 2–5 times the diameter of the nuclei in the embryo. The upper part of the protoplasmatic stratum contains numerous small and a few larger yolk-grains, and contains near and under the embryo small nuclei; the middle part of the stratum contains the vacuoles, the big nuclei, and but few yolk grains; the deepest part contains larger granules, and merges gradually into the yolk proper (see also His, 18, 75, and Rückert, 32). Rückert designates these nuclei as "*Merocytenkerne*," and the cells which they represent as "*Merocyten*." The special function of the protoplasmic layer appears to be the assimilation of the nutritive yolk. Rückert also maintains, but without proper evidence, it seems to me, that merocytes become cells, some of which join the ectoderm, some the entoderm, and yet others the mesenchyma. In the *Sauropsida* we find similar nuclei and similar relations of the nucleated layer, but in this type the protoplasmic layer becomes the epithelium of the yolk (see especially H. Strahl, 40), and I consider it probable that these parablastic nuclei in all meroblastic ova belong to the vitelline entoderm.

In holoblastic mammalian ova the vitelline entoderm is cellular, and no nuclei are known similar to the large "parablastic" nuclei of mesoblastic ova.

⁵ From sections in the collection of Prof. His, which he generously permitted me to study.

AUTHORITIES CITED.

1. AGASSIZ, A., and WHITMAN, C. O. On the Development of Some Pelagic Fish Eggs. Preliminary notice. Proc. Am. Acad., XX., pp. 23-75, 1 Pl., 1884.
2. BALFOUR, F. M. A Monograph on the Development of the Elasmobranch Fishes. London, pp. 295, Pls. I.-XX., 1878.
3. BAMBECKE, V. Recherches sur le Développement du Pélobate Brun (*Pelobates fusus* Wagl.). Mem. Couron. Belg. Acad., XXXIV., 66 pp., 5 Pls., 1868.
4. BENEDEN, E. VAN, and JULIN, CHARLES. Recherches sur la Formation des Annexes Foetales chez les Mammifères (Lapin et Cheiropères). Arch. Biol., V., fasc. 3, 369-434, Pls. XX.-XXIV., 1884.
5. BELLONCI, GUISEPPE. Blastoporo e linea primitiva dei Vertebrati. R. Acad. Lincei. Ser. 3, XIX., CCLXXXI., pp. 45. Taf. I.-VI., 1884.
6. BONNET, R. Beiträge zur Embryologie der Wiederkauer gewonnen am Schafen. Arch. f. Anat. u. Entwickl., Anat. Abth., 170-230. Taf. IX.-XI., 1884.
7. CARIUS, FR. Ueber die Entwicklung der Chorda und der Primitiven Rachenhaut bei Meerschweinchen und Kaninchen. 8vo, pp. 33. Taf. I., Marburg, 1888.
8. DUVAL, MATTHIAS. De la Formation du Blastoderme dans l'oeuf d'oiseau. Ann. Sci. Nat. Zool., XVIII., Ser. 6, 1-208, Pls. I.-V., 1884.
9. GOETTE, A. Der Keim des Forelleneies (Beiträge zur Entwicklungsgeschichte der Wirbelthiere). M. Schultze's Arch. f. Mikr. Anat., IX., 679-708. Taf. XXVII., 1873.
10. ——. Die Entwicklungsgeschichte der Unke (*Bombinator igneus*) als Grundlage einer Vergleichenden Morphologie der Wirbelthiere. 8vo, p. 964. 4to, Atlas. Taf. XXII., Leipzig, 1875.
11. HEAPE, W. The Development of the Mole (*Talpa europea*). The Formation of the Germinal Layers, and Early Development of the Medullary Groove and Notochord. Q. J. M. S., XXIII., 412-452, Pls. XXVIII.-XXXI. Studies Morph. Lab. Cambridge, II., 29-75, Pls. VI.-IX., 1883.
12. HERTWIG, O. Die Entwicklung der mittleren Keimblattes der Wirbelthiere. Jen. Z., XV., 286-340. Taf. XII.-XV., 1882.
13. ——. Die Entwicklung des mittleren Keimblattes der Wirbelthiere. Jena Z. Natur., XVI., 247-328. Taf. XIV.-XVIII., 1883.
14. HERTWIG, O. u. R. Die Coelom theorie: Versuch einer Erklärung des mittleren Keimblattes. Jena Zeitsch., XV., 1-150. Taf. I.-III., 1881.
15. HIS, W. Die Häute und Höhlen des Körpers. Basel, 34, 1865.
16. ——. Untersuchungen über die erste Anlage des Wirbelthierleibes. Die erste Entwicklung des Hühnchens im Ei. Leipzig, 237 pp., 12 Taf., 1868.

17. —. Der Keimwall des Hühnereies und die Entstehung der Parablastischen Zellen. *Zeitsch. f. Anat. u. Entwickl.*, I., 274–287, 1876.
18. —. Die Lehre von einem Bidesubstanzkeim (Parablast). Rückblick nebst Besprechung einiger neuerer Entwicklungsgeschichtlicher Arbeiten. *Arch. f. Anat. u. Phys., Anat. Abth.*, 62–108, 1882.
19. KÖLLIKER, A. Ueber die Nichtexistenz eines Embryonalen Bindegewebskeims (Parablasts). *Sitzb. Phys. Med. Ges. Würzburg*, 14–18, 1884.
20. —. Die Embryonalen Keimblätter und die Gewebe (und Nachtrag). *Z. Z.*, XL., 179–213. *Taf. XI.–XII.*, 336–357, 1884.
21. —. Kollmann's Akroblast. *Z. Z.*, XLI., 155–158, 1885.
22. KOLLMANN, J. Der Mesoblast und die Entwicklung der Gewebe bei Wirbelthieren. *Biol. Centrabl.*, III., No. 24, pp. 737–747, 1884.
23. —. Der Randwulst und der Ursprung der Stützsubstanz (und Nachwort). *Arch. f. Anat. u. Phys., Anat. Abth.*, 341–434. *Taf. XVI.–XVIII.*, 461–465, 1884.
24. —. Gemeinsame Entwicklungsbahnen der Wirbelthiere. *His's Arch.*, 279–306. *Taf. XII.*, 1885.
25. —. Ueber Gemeinsame Entwicklungsbahnen der Wirbelthiere. *Zeit. Wiss. Zool.*, XLI., 517–524, 1885.
26. KOWALEWSKI, MIECZ VON. Ueber die ersten Entwicklungsprocess der Knochenfische. *Z. Z.*, XLIII., 434–480. *Taf. XVII.*, 1886.
27. LAMPERT, K. Zur Genese der Chorda Dorsalis beim Axolotl. *Sitzb. Phys. Med. Soc. Erlangen*, 37–57. *Taf. I.*, 1883.
- 27a. LANKESTER, E. RAY. Notes on Embryology and Classification. *Quar. Jour. Micr. Sci.*, XVII., 399–454, Pl. XXV., 1877.
28. LIEBERKÜHN, N. Ueber die Chorda Sangethieren. *Arch. f. Anat. u. Phys., Anat. Abth.*, 399–438. *Taf. XX.–XXI.*, 1882.
29. RABL, CARL. Theorie des Mesoderms. *Morph. Jb.*, XV., 113–250. *Taf. VII.–X.*, 1889.
30. RAUBER, A. Ueber den Ursprung des Blutes und der Bidesubstanzen. *Sitzb. Natforsch. Ges., Leipzig*, 1877.
31. —. Die Entwicklung der Gewebe und die Sitz. *Natforsch. Ges., Leipzig*, 1883.
32. RÜCKERT, J. Zur Keimblattbildung bei Selachiern Ein Beitrag zur Lehre vom Parablast. 8vo, pp. 58, München, 1885.
33. —. Ueber die Anlange des Mittleren Keimblattes und die erste Blutbildung bei Torpedo. *Anat. Anz.*, II., No. 4, pp. 97–112; No. 6, 154–176, 1887.
34. RYDER, JOHN A. A Contribution to the Embryology of Osseous Fishes, with Special Reference to the Development of the Cod (*Gadus morhua*). *Ann. Rept. Com. Fish and Fisheries for 1882. Pls. I.–XII.*, 1884.
35. SCHULTZE, OSKAR. Die Entwicklung der Keimblätter und der Chorda Dorsalis von *Rana fusca*. *Zeit. Wiss. Zool.*, XLVII., 325–352. *Taf. XXVIII.–XXIX.*, 1888.

36. SCHWARZ, D. Untersuchungen der Schwanzendes bei Embryonen der Wirbelthiere. Zeit. Wiss. Zool., XLVIII., Heft 2, 191-224. Taf. XII.-XIV., 1889.

37. SELENKA, E. Studien über Entwicklungsgeschichte der Thiere, Heft IV. Das Opossum (*Didelphys virginiana*). 1 Hälfte, Wiesbaden, 1886.

38. SHIPLEY, ARTHUR E. On Some Points in the Development of *Petromyzon fluviatilis*. Quar. Jour. Micr. Sci., XXVII., 325-370. Pls. XXVI.-XXIX. Studies Morph. Lab. Cambridge, IV., 173-218, Pls. XVIII.-XXI., 1888.

39. STRAHL, H. Beiträge zur Entwicklung der Reptilien. His's Arch., Anat. Abth., 1-43. Taf. I., 1883.

40. —. Die Dottersackswand und der Parablast der Eidechse. Z. Z., XLV., No. 1, 283-307. Taf. XVI., 1887.

41. SWAEN, A. Etudes sur le Développement de la Torpille (*Torpedo ocellata*). Arch. de Biol., VII., 537-585, Pls. XIV.-XVI., 1887.

42. WALDEYER, W. Archiblast and Parablast. Arch. f. Mikr. Anat., XXII., 1-77. Z. thiel Allgemeine Anatomie, 1883.

43. WELDON, A. B. Note on the Early Development of *Lacerta muralis*. Q. J. M. S., XXIII., 134-144, Pls. IV.-VI. Also in Sedgwick's Studies, II., 1-12, Pls. I.-III., 1883.

44. WILL, L. Bericht über Studien zur Entwicklungsgeschichte von *Platydictylus mauritanicus*. Sitzb. Kon. Preus. Akad. Wiss. Berlin, LII., 1121-1228, 1889.

45. ZIEGLER, H. E. Die Embryonale Entwicklung bei *Salmo salar*. Freiburg (Diss.), 1882.

46. ZUMSTEIN, J. J. Ueber das Mesoderm der Vogelkeimscheibe (Huhn und Ente). 8 vo., p. 56. Bern (Inaug. Diss.), 1887